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Approximation by the Legendre collocation method of a model problem in electrophysiology

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Abstract

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We examine the polynomial approximation of the solution of a nonlinear differential problem modelling the evolution of the potential inside an electrically stimulated neuron. The collocation method at the Legendre Gauss–Lobatto nodes is used for the discretization with respect to the space variable.

Keywords: Spectral methods; Legendre polynomials; partial differential equations.

1. Elementary exposition of the physiological environment

The purpose of this paper is to numerically simulate the potential diffusion inside a *neuron* of a vertebrate central nervous system, under the action of suitable external stimulations. Information about the electric conduction properties of the neurons is provided in [8]. A relatively simplified structure is recognized in the *cerebellar granule cells*. Referring to Fig. 1.1, these are constituted by a central core (*soma*) emitting a mean of four conductive filaments (*dendrites*).

The current flow is activated by the so-called *synapses*, situated at the far end of each dendrite, establishing the connection with other neurons. In the electrophysiological experiments, the synapses receive an excitatory input originating from the next neurons and successively transmitted to the soma. The activation of the synapses generally follows a nonlinear law when influencing the potential evolution in the cell.

A differential model, where the dendrites are assumed to be one-dimensional, will be considered in the following sections.

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2. The model equations

A mathematical setting to describe the evolution of the potential inside a cerebellar cell can be introduced (see [5]). We denote by $M \geqslant 1$ the number of dendrites connected to the soma. The length of each dendrite is equal to l_m, $1 \leqslant m \leqslant M$. Thus, according to [8], the corresponding potential $U_m : [0, l_m] \times [0, T[\rightarrow \mathbb{R}$, $1 \leqslant m \leqslant M$, satisfies the linear parabolic equation

$$\frac{\partial U_m}{\partial t} = \zeta_m \frac{\partial^2 U_m}{\partial x^2} - \mu_m U_m, \quad \text{in }]0, l_m[\times]0, T[, \tag{2.1}$$

where ζ_m, μ_m, $1 \leqslant m \leqslant M$, are positive constants depending on the electrical properties of the dendritic fibers. For $1 \leqslant m \leqslant M$, we provide the initial conditions

$$U_m(x, 0) = f_m(x), \quad x \in]0, l_m[. \tag{2.2}$$

The following conditions will be assumed at the end of the dendrites:

$$\nu \frac{\partial U_m}{\partial x}(l_m, t) + g_m(t) = 0, \quad t \in]0, T[, \ 1 \leqslant m \leqslant M. \tag{2.3}$$

Here, $g_m :]0, T[\rightarrow \mathbb{R}$ are given regular functions and $\nu > 0$. Later, in Section 6, we shall assume a nonlinear response of these boundary points due to the stimulated synapses. Finally, the different equations are coupled at the point $x = 0$ in view of the relations

$$U_{m_1}(0, t) = U_{m_2}(0, t), \quad t \in]0, T[, \ 1 \leqslant m_1 \leqslant m_2 \leqslant M, \tag{2.4}$$

$$\sum_{m=1}^{M} \nu_m \frac{\partial U_m}{\partial x}(0, t) + \gamma(t) = 0, \quad t \in]0, T[, \ 1 \leqslant m \leqslant M, \tag{2.5}$$

ν_m, $1 \leqslant m \leqslant M$, being some given positive constants which have the physical dimension of a length divided by an impedance. The function $\gamma :]0, T[\rightarrow \mathbb{R}$ is a suitable current excitement acting at the soma.

By updating the values of the different parameters, it is not restrictive to assume that the dendrites are all of the same length. Therefore, henceforth we shall set $l_m = 2$, $1 \leqslant m \leqslant M$, where the unity of measure is expressed in $10 \times \mu$m.

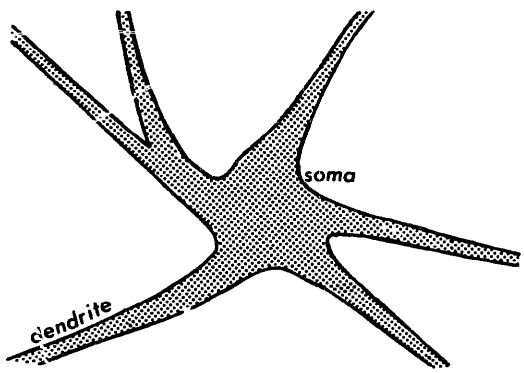

Fig. 1.1. Structure of a cerebellar cell.

We examine in the coming sections the approximation of the equations presented above by algebraic polynomials, using the collocation method at the Legendre Gauss–Lobatto nodes.

3. The numerical approach: preliminary considerations

In the *collocation method* the solution of a boundary value problem is approximated by a polynomial of prescribed degree n satisfying the differential equation and the boundary conditions in a set of $n+1$ nodes. To achieve high accuracy, these nodes are usually related to some Gaussian integration formula. The way to implement the collocation method is described, for instance, in [1,3]. Here, in order to establish the notations, we recall some basic facts.

For $n \geqslant 1$, we use as collocation nodes the points $\eta_j^{(n)}$, $0 \leqslant j \leqslant n$, where $\eta_0^{(n)} = 0$, $\eta_n^{(n)} = 2$ and $\eta_j^{(n)} - 1$, $1 \leqslant j \leqslant n-1$, are the zeros of P_n', P_n being the Legendre polynomial of degree n. This choice leads to the integration formula

$$\int_0^2 q \, \mathrm{d}x = \sum_{j=0}^{n} q\left(\eta_j^{(n)}\right) \tilde{w}_j^{(n)}, \tag{3.1}$$

which is true for any polynomial q of degree at most $2n-1$. It is well known that the weights $\tilde{w}_j^{(n)}$, $0 \leqslant j \leqslant n$, are positive.

The kernel in the implementation of the collocation method is the construction of an $(n+1) \times (n+1)$ matrix representing the derivative operator in the space $\mathscr{P}_n$ of polynomials of degree at most n, with respect to the set of nodes. This matrix is given by $\tilde{D}_n^{(1)} = \{\tilde{d}_{ij}^{(1)}\}_{0 \leqslant i \leqslant n, 0 \leqslant j \leqslant n} := \{(\mathrm{d}/\mathrm{d}x)\tilde{l}_j^{(n)}(\eta_i^{(n)})\}_{0 \leqslant i \leqslant n, 0 \leqslant j \leqslant n}$, where $\tilde{l}_j^{(n)}$, $0 \leqslant j \leqslant n$, are the Lagrange polynomials of degree n relative to the points $\eta_i^{(n)}$, $0 \leqslant i \leqslant n$. The computation of the entries of $\tilde{D}_n^{(1)}$ is easy and cheap by using basic properties of the Legendre polynomials. According to [3], we have

$$\tilde{d}_{ij}^{(1)} = \begin{cases} -\frac{1}{4}n(n+1), & i = j = 0, \\ \dfrac{P_n\left(\eta_i^{(n)}\right)}{P_n\left(\eta_j^{(n)}\right)} \dfrac{1}{\eta_i^{(n)} - \eta_j^{(n)}}, & i \neq j, \\ 0, & 1 \leqslant i = j \leqslant n-1, \\ \frac{1}{4}n(n+1), & i = j = n. \end{cases} \tag{3.2}$$

The second-order derivative operator $\tilde{D}_n^{(2)} = \{\tilde{d}_{ij}^{(2)}\}_{0 \leqslant i \leqslant n, 0 \leqslant j \leqslant n}$ is obtained by squaring $\tilde{D}_n^{(1)}$. Finally, we recall that, for any $q \in \mathscr{P}_n$, the following inequality holds:

$$\int_0^2 q^2 \, \mathrm{d}x \leqslant \sum_{j=0}^{n} q^2\left(\eta_j^{(n)}\right) \tilde{w}_j^{(n)} \leqslant 3 \int_0^2 q^2 \, \mathrm{d}x. \tag{3.3}$$

4. Numerical approximation of the differential problem

In order to approximate the solution of the problem of Section 2, we use the Legendre collocation method to deal with the variable x, and a standard implicit finite-difference scheme to advance in time.

For $K \geqslant 1$, let $h = T/K$ denote the time step. For any $1 \leqslant m \leqslant M$, we construct a sequence of polynomials $p_m^{(k)} \in \mathscr{P}_n$, $0 \leqslant k \leqslant K$. In particular, (2.1) is discretized as follows:

$$\frac{1}{h}\left[p_m^{(k+1)}(\eta_i^{(n)}) - p_m^{(k)}(\eta_i^{(n)}) \right] = \zeta_m \frac{\mathrm{d}^2}{\mathrm{d}x^2} p_m^{(k+1)}(\eta_i^{(n)}) - \mu_m p_m^{(k+1)}(\eta_i^{(n)}),$$
$$1 \leqslant i \leqslant n-1, \tag{4.1}$$

with the initial guess

$$p_m^{(0)}(\eta_i^{(n)}) = f_m(\eta_i^{(n)}), \quad 0 \leqslant i \leqslant n. \tag{4.2}$$

The boundary conditions at the endpoints of the dendrites will be

$$\frac{1}{h}\left[p_m^{(k+1)}(\eta_n^{(n)}) - p_m^{(k)}(\eta_n^{(n)}) \right] = \zeta_m \frac{\mathrm{d}^2}{\mathrm{d}x^2} p_m^{(k+1)}(\eta_n^{(n)}) - \mu_m p_m^{(k+1)}(\eta_n^{(n)})$$
$$- \omega_n \zeta_m \left[\frac{\mathrm{d}}{\mathrm{d}x} p_m^{(k+1)}(\eta_n^{(n)}) + \frac{1}{\nu} g_m(h(k+1)) \right], \tag{4.3}$$

where the positive constant ω_n will be specified later. Equation (4.3) is a linear combination of the differential equation at the boundary and the boundary condition itself. As we shall see, it is suggested by a variational formulation of the discrete problem. In addition, the use of (4.3), instead of imposing the exact boundary condition $(\mathrm{d}/\mathrm{d}x)p_m^{(k+1)}(\eta_n^{(n)}) + \nu^{-1} g_m(h(k+1)) = 0$, generally provides better numerical results.

In the same way, we can deal with the conditions at the soma. Namely, we require that

$$p_{m_1}^{(k+1)}(\eta_0^{(n)}) = p_{m_2}^{(k+1)}(\eta_0^{(n)}), \quad 0 \leqslant m_1 \leqslant m_2 \leqslant M, \tag{4.4}$$

$$\sum_{m=1}^{M} \frac{\nu_m}{\zeta_m h} \left[p_m^{(k+1)}(\eta_0^{(n)}) - p_m^{(k)}(\eta_0^{(n)}) \right]$$
$$= \sum_{m=1}^{M} \nu_m \left\{ \frac{\mathrm{d}^2}{\mathrm{d}x^2} p_m^{(k+1)}(\eta_0^{(n)}) - \frac{\mu_m}{\zeta_m} p_m^{(k+1)}(\eta_0^{(n)}) + \omega_n \frac{\mathrm{d}}{\mathrm{d}x} p_m^{(k+1)}(\eta_0^{(n)}) \right\}$$
$$+ \omega_n \gamma(h(k+1)). \tag{4.5}$$

The set of equations proposed here is equivalent to a linear system of dimension $m(n+1)$ in the unknowns $p_m^{(k+1)}(\eta_j^{(n)})$, $0 \leqslant j \leqslant n$, $1 \leqslant m \leqslant M$. One can verify that the corresponding matrix is positive definite. At the end of computation we expect $p_m^{(k+1)}$, $1 \leqslant k \leqslant K-1$, $1 \leqslant m \leqslant M$, to be a suitable approximation of the function $U_m(\cdot, h(k+1))$.

An analysis of convergence of the algorithm can be developed. The starting point is the possibility of writing the discrete problem in a variational way. To this end, we define the parameter ω_n as the inverse of the weights in (3.1) relative to the endpoints, i.e., $\omega_n = [\tilde{w}_0^{(n)}]^{-1} = [\tilde{w}_n^{(n)}]^{-1} = \frac{1}{2}n(n+1)$.

For $1 \leqslant m \leqslant M$, let $\phi_m \in \mathscr{P}_n$ denote M test functions satisfying $\phi_{m_1}(\eta_0^{(n)}) = \phi_{m_2}(\eta_0^{(n)})$, $1 \leqslant m_1 \leqslant m_2 \leqslant M$. Then, a linear combination of (4.1), (4.3) and (4.5) yields

$$\sum_{m=1}^{M} \frac{\nu_m}{\zeta_m h} \sum_{i=0}^{n} \left[p_m^{(k+1)}(\eta_i^{(n)}) - p_m^{(k)}(\eta_i^{(n)}) \right] \phi_m(\eta_i^{(n)}) \tilde{w}_i^{(n)}$$
$$= \sum_{m=1}^{M} \nu_m \left[\sum_{i=0}^{n} \frac{\mathrm{d}^2}{\mathrm{d}x^2} p_m^{(k+1)}(\eta_i^{(n)}) \phi_m(\eta_i^{(n)}) \tilde{w}_i^{(n)} - \frac{\mu_m}{\zeta_m} \sum_{i=0}^{n} p_m^{(k+1)}(\eta_i^{(n)}) \phi_m(\eta_i^{(n)}) \tilde{w}_i^{(n)} \right.$$
$$\left. + \frac{\mathrm{d}}{\mathrm{d}x} p_m^{(k+1)}(\eta_0^{(n)}) \phi_m(\eta_0^{(n)}) - \frac{\mathrm{d}}{\mathrm{d}x} p_m^{(k+1)}(\eta_n^{(n)}) \phi_m(\eta_n^{(n)}) \right]$$

$$-\frac{1}{\nu}\sum_{m=1}^{M}\nu_m g_m(h(k+1))\phi_m(\eta_n^{(n)})+\frac{1}{M}\sum_{m=1}^{M}\gamma(h(k+1))\phi_m(\eta_0^{(n)})$$

$$=-\sum_{m=1}^{M}\nu_m\left[\int_0^2\frac{\mathrm{d}}{\mathrm{d}x}p_m^{(k+1)}\frac{\mathrm{d}}{\mathrm{d}x}\phi_m\,\mathrm{d}x+\frac{\mu_m}{\zeta_m}\sum_{i=0}^{n}p_m^{(k+1)}(\eta_i^{(n)})\phi_m(\eta_i^{(n)})\tilde{w}_i^{(n)}\right]$$

$$-\frac{1}{\nu}\sum_{m=1}^{M}\nu_m g_m(h(k+1))\phi_m(\eta_n^{(n)})+\frac{1}{M}\sum_{m=1}^{M}\gamma(h(k+1))\phi_m(\eta_0^{(n)}). \tag{4.6}$$

The last inequality has been obtained thanks to formula (3.1) and integration by parts.

Stability and convergence of the scheme are recovered with arguments similar to those used in [2]. The error estimates show a spectral type convergence behavior for the approximation with respect to the variable x (i.e., the error decays with a rate depending on the regularity of the exact solution and it is exponential for analytic solutions), and convergence of order one with respect to the variable t, with no restrictions on the time step. The proof is quite technical, thus we describe the fundamental steps. We start by defining the spaces

$$X=\Big\{\phi\in\left[H^1(0,2)\right]^M \mid \phi_{m_1}(0)=\phi_{m_2}(0),\ 1\leqslant m_1\leqslant m_2\leqslant M,$$

$$\phi_m \text{ being the restriction of } \phi \text{ to the } m\text{th dendrite}\Big\},$$

$$X_n=\{\phi\in X \mid \phi_m\in\mathscr{P}_n,\ 1\leqslant m\leqslant M\}.$$

We note that a weak formulation of problem (2.1)–(2.5) is

$$\sum_{m=1}^{M}\frac{\nu_m}{\zeta_m}\int_0^2\frac{\partial U_m}{\partial t}\phi_m\,\mathrm{d}x=-\sum_{m=1}^{M}\nu_m\left[\int_0^2\frac{\partial U_m}{\partial x}\frac{\mathrm{d}\phi_m}{\mathrm{d}x}\,\mathrm{d}x+\frac{\mu_m}{\zeta_m}\int_0^2 U_m\phi_m\,\mathrm{d}x\right]$$

$$-\frac{1}{\nu}\sum_{m=1}^{M}\nu_m g_m(t)\phi_m(2)+\frac{1}{M}\sum_{m=1}^{M}\gamma(t)\phi_m(0),$$

$$t\in]0,T[,\ \forall\phi\in X. \tag{4.7}$$

Then, we define the projection operator $\Pi_n: X\to X_n$ by

$$\sum_{m=1}^{M}\nu_m\left[\int_0^2\frac{\partial}{\partial x}(U_m-\Pi_n U_m)\frac{\mathrm{d}\phi_m}{\mathrm{d}x}\,\mathrm{d}x+\frac{\mu_m}{\zeta_m}\int_0^2(U_m-\Pi_n U_m)\phi_m\,\mathrm{d}x\right]=0, \tag{4.8}$$

for any $\phi\in X_n$.

Now, we introduce the errors $\epsilon_m^{(k)}(x)=p_m^{(k)}(x)-\Pi_n U_m(x,hk)$, $x\in[0,2]$, $0\leqslant k\leqslant K$, $1\leqslant m\leqslant M$. Thanks to (3.1), (4.6)–(4.8) we have for $\phi_m=\epsilon_m^{(k+1)}$, $1\leqslant m\leqslant M$:

$$\sum_{m=1}^{M}\frac{\nu_m}{\zeta_m h}\sum_{i=0}^{n}\left[\epsilon_m^{(k+1)}(\eta_i^{(n)})-\epsilon_m^{(k)}(\eta_i^{(n)})\right]\epsilon_m^{(k+1)}(\eta_i^{(n)})\tilde{w}_i^{(n)}$$

$$+\sum_{m=1}^{M}\nu_m\left[\int_0^2\left(\frac{\mathrm{d}}{\mathrm{d}x}\epsilon_m^{(k+1)}\right)^2\mathrm{d}x+\frac{\mu_m}{\zeta_m}\sum_{i=0}^{n}(\epsilon_m^{(k+1)})^2(\eta_i^{(n)})\tilde{w}_i^{(n)}\right]+E_n^{(k+1)}=0, \tag{4.9}$$

where

$$
\begin{aligned}
E_n^{(k+1)} = \sum_{m=1}^{M} \frac{\nu_m \mu_m}{\zeta_m} \Bigg[& \sum_{i=0}^{n} \Pi_n U_m(\eta_i^{(n)}, h(k+1)) \epsilon_m^{(k+1)}(\eta_i^{(n)}) \tilde{w}_i^{(n)} \\
& - \int_0^2 \Pi_n U_m(x, h(k+1)) \epsilon_m^{(k+1)}(x)\, \mathrm{d}x \Bigg] \\
+ \sum_{m=1}^{M} \frac{\nu_m}{\zeta_m} \sum_{i=0}^{n} \Bigg[& \frac{U_m(\eta_i^{(n)}, h(k+1)) - U_m(\eta_i^{(n)}, hk)}{h} \\
& - \frac{\partial U_m}{\partial t}(\eta_i^{(n)}, h(k+1)) \Bigg] \epsilon_m^{(k+1)}(\eta_i^{(n)}) \tilde{w}_i^{(n)} \\
+ \sum_{m=1}^{M} \frac{\nu_m}{\zeta_m} \Bigg[& \sum_{i=0}^{n} \frac{\partial U_m}{\partial t}(\eta_i^{(n)}, h(k+1)) \epsilon_m^{(k+1)}(\eta_i^{(n)}) \tilde{w}_i^{(n)} \\
& - \int_0^2 \frac{\partial U_m}{\partial t}(x, h(k+1)) \epsilon_m^{(k+1)}(x)\, \mathrm{d}x \Bigg] \\
- \sum_{m=1}^{M} \frac{\nu_m}{\zeta_m h} & \sum_{i=0}^{n} \left[U_m(\eta_i^{(n)}, h(k+1)) - \Pi_n U_m(\eta_i^{(n)}, h(k+1)) \right] \epsilon_m^{(k+1)}(\eta_i^{(n)}) \tilde{w}_i^{(n)} \\
+ \sum_{m=1}^{M} \frac{\nu_m}{\zeta_m h} & \sum_{i=0}^{n} \left[U_m(\eta_i^{(n)}, hk) - \Pi_n U_m(\eta_i^{(n)}, hk) \right] \epsilon_m^{(k+1)}(\eta_i^{(n)}) \tilde{w}_i^{(n)}.
\end{aligned}
$$

By virtue of (3.3) and the Schwarz inequality, (4.9) implies

$$
\begin{aligned}
\left(\sum_{m=1}^{M} \frac{\nu_m}{\zeta_m} \int_0^2 [\epsilon_m^{(k+1)}]^2\, \mathrm{d}x \right)^{1/2} \leqslant & \, 3 \left(\sum_{m=1}^{M} \frac{\nu_m}{\zeta_m} \int_0^2 [\epsilon_m^{(k)}]^2\, \mathrm{d}x \right)^{1/2} \\
& + h \left(\sum_{m=1}^{M} \frac{\nu_m}{\zeta_m} \int_0^2 [\epsilon_m^{(k+1)}]^2\, \mathrm{d}x \right)^{-1/2} |E_n^{(k+1)}|. \qquad (4.10)
\end{aligned}
$$

An estimate of the terms $\| \epsilon_m^{(k+1)} \|_{L^2(0,2)}$, $1 \leqslant m \leqslant M$, $0 \leqslant k \leqslant K-1$, is then obtained by the discrete counterpart of the Gronwall lemma and by showing that the second term on the right-hand side of (4.10) tends to zero for $n \to +\infty$ and $h \to 0$ with a rate depending on the smoothness of U_m, $1 \leqslant m \leqslant M$ (see [3] for the details concerning the treatment of the projection operator). The final error estimate is recovered by the triangle inequality

$$
\begin{aligned}
& \| p_m^{(k+1)} - U_m(\cdot, h(k+1)) \|_{L^2(0,2)} \\
& \quad \leqslant \| \epsilon_m^{(k+1)} \|_{L^2(0,2)} + \| (U_m - \Pi_n U_m)(\cdot, h(k+1)) \|_{L^2(0,2)}, \quad 1 \leqslant m \leqslant M. \qquad (4.11)
\end{aligned}
$$

Again, the last term in (4.11) tends to zero for $n \to +\infty$. Convergence in the norm of $L^2(H^1(0, 2))$ is also obtained by (4.9).

5. Implementation of the scheme

A practical approach to solve the system corresponding to equations (4.1)–(4.5) is to evaluate the contribution of the potential independently in each dendrite, and accordingly update the common value at the soma. This can be done in the following way. At each step, for any $1 \leqslant m \leqslant M$, we define two auxiliary problems. In the first one, we seek $r_m^{(k+1)} \in \mathscr{P}_n$ satisfying

$$\frac{1}{h} r_m^{(k+1)}(\eta_i^{(n)}) = \zeta_m \frac{d^2}{dx^2} r_m^{(k+1)}(\eta_i^{(n)}) - \mu_m r_m^{(k+1)}(\eta_i^{(n)}), \quad 1 \leqslant i \leqslant n-1, \tag{5.1}$$

with the boundary constraints

$$r_m^{(k+1)}(\eta_0^{(n)}) = 1, \tag{5.2}$$

$$\frac{1}{h} r_m^{(k+1)}(\eta_n^{(n)}) = \zeta_m \frac{d^2}{dx^2} r_m^{(k+1)}(\eta_n^{(n)}) - \mu_m r_m^{(k+1)}(\eta_n^{(n)}) - \omega_n \zeta_m \frac{d}{dx} r_m^{(k+1)}(\eta_n^{(n)}). \tag{5.3}$$

In the second one, we seek $s_m^{(k+1)} \in \mathscr{P}_n$ satisfying

$$\frac{1}{h}\left[s_m^{(k+1)}(\eta_i^{(n)}) - p_m^{(k)}(\eta_i^{(n)})\right] = \zeta_m \frac{d^2}{dx^2} s_m^{(k+1)}(\eta_i^{(n)}) - \mu_m s_m^{(k+1)}(\eta_i^{(n)}),$$
$$1 \leqslant i \leqslant n-1, \tag{5.4}$$

with the boundary conditions

$$s_m^{(k+1)}(\eta_0^{(n)}) = 0, \tag{5.5}$$

$$\frac{1}{h}\left[s_m^{(k+1)}(\eta_n^{(n)}) - p_m^{(k)}(\eta_n^{(n)})\right] = \zeta_m \frac{d^2}{dx^2} s_m^{(k+1)}(\eta_n^{(n)}) - \mu_m s_m^{(k+1)}(\eta_n^{(n)})$$
$$- \omega_n \zeta_m \left[\frac{d}{dx} s_m^{(k+1)}(\eta_n^{(n)}) + \frac{1}{\nu} g_m(h(k+1))\right]. \tag{5.6}$$

It is not difficult to realize that both (5.1)–(5.3) and (5.4)–(5.6) admit a unique polynomial solution, since they are related to some coercive bilinear form. The entries of the matrices of the corresponding systems are easily obtained with the help of the coefficients $\tilde{d}_{ij}^{(1)}$, $\tilde{d}_{ij}^{(2)}$ introduced in Section 3.

Now we note that

$$p_m^{(k+1)} = \alpha_{k+1} r_m^{(k+1)} + s_m^{(k+1)}, \quad \text{where } \alpha_{k+1} = p_m^{(k+1)}(\eta_0^{(n)}). \tag{5.7}$$

Finally, the value of α_{k+1} is obtained by substituting (5.7) in (4.5). Recalling (5.2) and (5.5), we get

$$\alpha_{k+1} = \left\{\omega_n \gamma(h(k+1)) + \sum_{m=1}^{M} \nu_m \left[\frac{\alpha_k}{\zeta_m h} + \frac{d^2}{dx^2} s_m^{(k+1)}(\eta_0^{(n)}) + \omega_n \frac{d}{dx} s_m^{(k+1)}(\eta_0^{(n)})\right]\right\}$$
$$\times \left\{\sum_{m=1}^{M} \nu_m \left[\frac{1}{\zeta_m h} - \frac{d^2}{dx^2} r_m^{(k+1)}(\eta_0^{(n)}) + \frac{\mu_m}{\zeta_m} - \omega_n \frac{d}{dx} r_m^{(k+1)}(\eta_0^{(n)})\right]\right\}^{-1}, \tag{5.8}$$

where, at the beginning of the process, we set $\alpha_0 = M^{-1} \Sigma_{m=1}^{M} f_m(\eta_0^{(n)})$.

The procedure described here allows the recovering of the approximated potential at the step $k+1$ by solving in parallel a set of $2M$ linear systems of order $(n+1)\times(n+1)$.

6. The nonlinear case

Generally, when the synapses are activated, the potential interacts nonlinearly with the current at the free ends of the dendrites. This phenomenon has been studied, for instance, in [6]. In this case, relation (2.3) takes the form

$$\nu\frac{\partial U_m}{\partial x}(l_m, t) + g_m(U_m(l_m, t)) = 0, \quad t \in]0, T[, \; 1 \leqslant m \leqslant M, \tag{6.1}$$

where $g_m : \mathbb{R} \to \mathbb{R}$ are given functions. The behavior of the current g_m (the dimensional constant $\nu > 0$ is a length over an impedance) is recovered by fitting the results of neurophysiological experiments. A typical shape of g_m is provided in Fig. 6.1, where the zero potential is assumed on the dendritic membrane.

An analysis of existence and uniqueness in the nonlinear case is given in [4]. Concerning the numerical approach, we simply modify relation (4.3) in the following way:

$$\frac{1}{h}\left[p_m^{(k+1)}(\eta_n^{(n)}) - p_m^{(k)}(\eta_n^{(n)})\right] = \zeta_m \frac{\mathrm{d}^2}{\mathrm{d}x^2} p_m^{(k+1)}(\eta_n^{(n)}) - \mu_m p_m^{(k+1)}(\eta_n^{(n)})$$
$$- \omega_n \zeta_m \left[\frac{\mathrm{d}}{\mathrm{d}x} p_m^{(k+1)}(\eta_n^{(n)}) + \frac{1}{\nu} g_m\left(p_m^{(k)}(\eta_n^{(n)})\right)\right]. \tag{6.2}$$

The nonlinear part is treated explicitly in order to allow the implementation of the scheme as described in Section 5. In this case, the term $\nu^{-1}g_m(p_m^{(k)}(\eta_n^{(n)}))$ replaces the term $\nu^{-1}g_m(h(k+1))$ in (5.6).

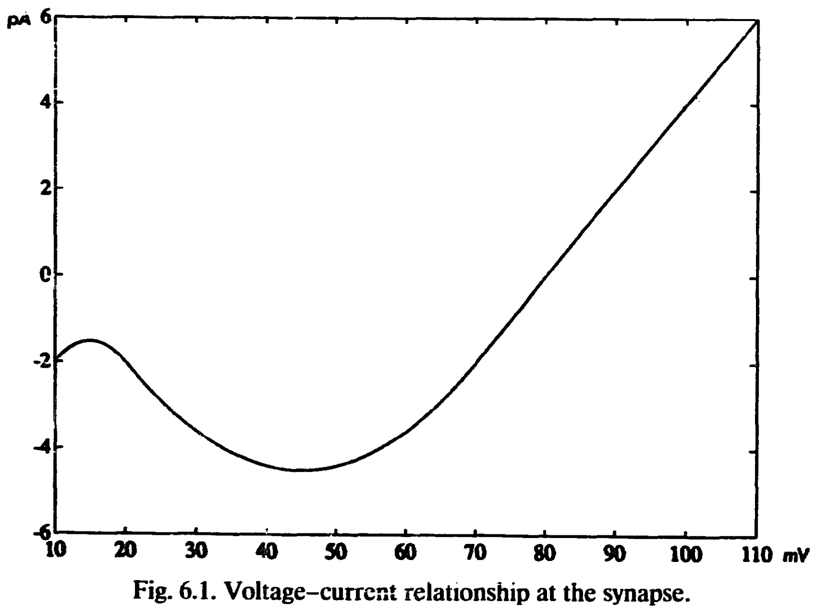

Fig. 6.1. Voltage–current relationship at the synapse.

A proof of convergence in the nonlinear case is obtained by adding to the right-hand side of (4.9) the term

$$\begin{aligned}
\Xi_n^{(k+1)} &= \frac{1}{\nu}\sum_{m=1}^{M} \nu_m\left[g_m\left(p_m^{(k)}(2)\right) - g_m\left(U_m(2, h(k+1))\right)\right]\epsilon_m^{(k+1)}(2)\\
&= \frac{1}{\nu}\sum_{m=1}^{M} \nu_m\left[g_m\left(p_m^{(k)}(2)\right) - g_m\left(\Pi_n U_m(2, hk)\right)\right]\epsilon_m^{(k+1)}(2)\\
&\quad + \frac{1}{\nu}\sum_{m=1}^{M} \nu_m\left[g_m\left(\Pi_n U_m(2, hk)\right) - g_m\left(U_m(2, hk)\right)\right]\epsilon_m^{(k+1)}(2)\\
&\quad + \frac{1}{\nu}\sum_{m=1}^{M} \nu_m\left[g_m\left(U_m(2, hk)\right) - g_m\left(U_m(2, h(k+1))\right)\right]\epsilon_m^{(k+1)}(2).
\end{aligned}$$

Recalling that for any polynomial $q \in \mathscr{P}_n$, one has

$$|q(2)| \leqslant 2n\, \| q \|_{L^2(0,2)}, \tag{6.3}$$

and assuming that g_m, $1 \leqslant m \leqslant M$, are Lipschitz functions (which seems to be a reasonable restriction in view of practical applications), it is easy to estimate $|\Xi_n^{(k+1)}|$. In particular, one has

$$\begin{aligned}
&\left|\frac{1}{\nu}\sum_{m=1}^{M} \nu_m\left[g_m\left(p_m^{(k)}(2)\right) - g_m\left(\Pi_m U_m(2, hk)\right)\right]\epsilon_m^{(k+1)}(2)\right|\\
&\quad\leqslant \frac{C}{\nu}\sum_{m=1}^{M} \nu_m\left|\epsilon_m^{(k)}(2)\epsilon_m^{(k+1)}(2)\right|\\
&\quad\leqslant \frac{4n^2C}{\nu}\sum_{m=1}^{M} \nu_m\left\|\epsilon_m^{(k)}\right\|_{L^2(0,2)}\left\|\epsilon_m^{(k+1)}\right\|_{L^2(0,2)}.
\end{aligned} \tag{6.4}$$

Taking into account this contribution, we can still apply the Gronwall lemma as done for (4.10), provided the stability condition $hn^2 < C^*$ is satisfied for some $C^* > 0$. The two remaining terms tend to zero according to the regularity of U_m, $1 \leqslant m \leqslant M$.

7. Numerical experiments

We report in this section the results of the numerical tests. We start by examining the linear case ($g_m \equiv 0$, $1 \leqslant m \leqslant M$). Initially, the cell is assumed to be at potential zero. Then, a squared current pulse (corresponding to the function γ in (2.5)) of width 50 μsec and amplitude 40 pA is applied to the soma. We take $M = 4$, $T = 200$ μsec, $\mu_m = 0.04$ [msec]$^{-1}$, $\nu_m = 1$ μm/GΩ, $1 \leqslant m \leqslant M$. The constants ζ_m, $1 \leqslant m \leqslant M$, vary in the range $200 \div 4000$ [μm]^2/msec. The polynomials degree is $n = 10$.

In Figs. 7.1 and 7.2 we plot the potential at the soma (S) and at the end of the first dendrite (D), i.e., $p_1^{(k)}(\eta_n^{(n)})$. In the first case all the ζ_m's are equal. In the second case we have $\zeta_1 > \zeta_2 = \zeta_3 = \zeta_4$, giving an higher conductivity in the first dendrite. Therefore, a faster potential grow is followed by the decay due to the discharge on the other dendrites.

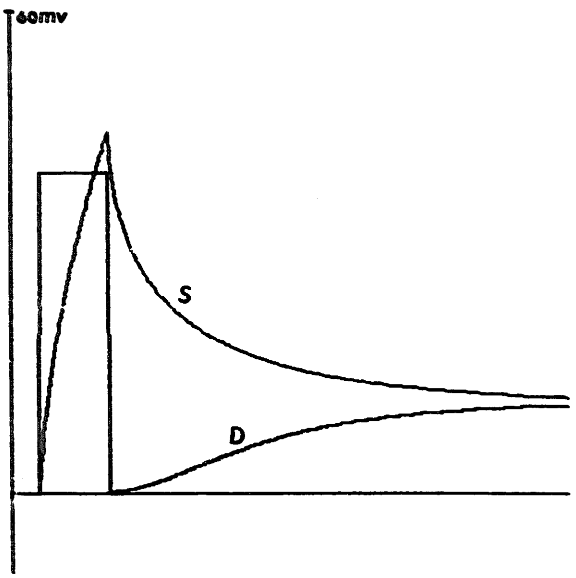

Fig. 7.1. Potential evolution for $\zeta_1 = \zeta_2 = \zeta_3 = \zeta_4$.

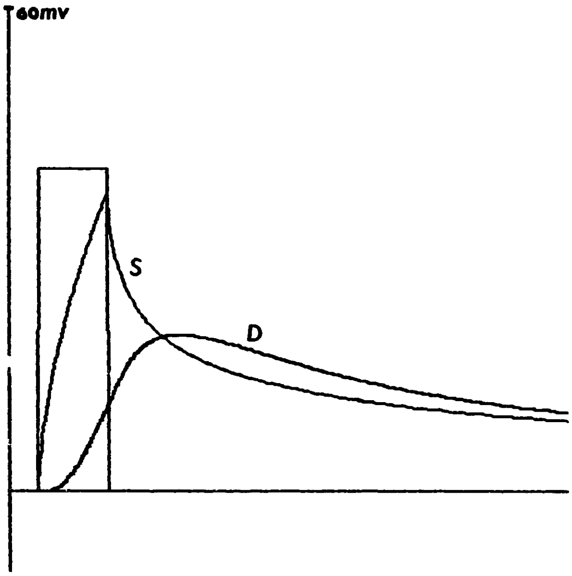

Fig. 7.2. Potential evolution for $\zeta_1 > \zeta_2 = \zeta_3 = \zeta_4$.

In the nonlinear case, the g_m's coincide with the function displayed in Fig. 6.1. For $M = 4$, the potential at the soma (S) and at the end of the first dendrite (D) are shown in Fig. 7.3, when one ($g_2 \equiv g_3 \equiv g_4 \equiv 0$), two ($g_3 \equiv g_4 \equiv 0$), three ($g_4 \equiv 0$), and four synapses are activated

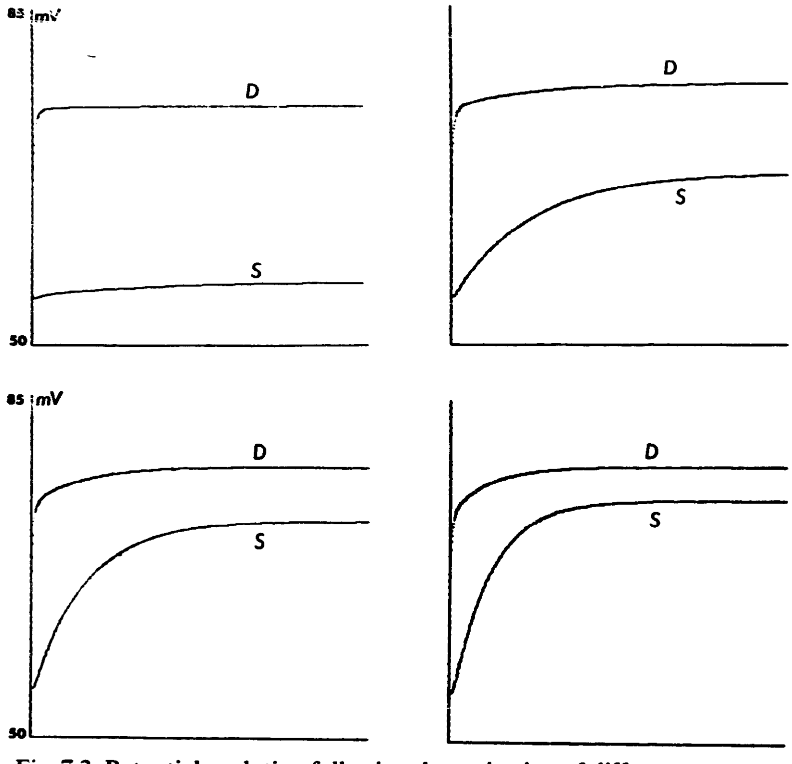

Fig. 7.3. Potential evolution following the activation of different synapses.

respectively. In this experiment we have $\zeta_m = 35000$ [μm]^2/msec, $\mu_m = 8$ [msec]$^{-1}$, $1 \leqslant m \leqslant M$. The initial potential is 55 mV. The other data are the same as those of the previous test. We note that, to better emphasize the behavior at the soma, these data have been chosen in order to have a dispersion of charge, due to the permeability of the dendritic membrane, higher than the standard value.

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